

SEASONAL CHANGE IN THE BREEDING BEHAVIOR OF THE MALE RED-WINGED BLACKBIRD

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CHANGES in behavior in response to changing conditions in the breeding situation have been demonstrated for a number of species. For species in which both sexes are directly involved in rearing the young, the changing features of the nest situation, such as the appearance of eggs or the hatching of young, have been shown to play a critical role in pacing behavioral change in both sexes (Lehrman, 1961; and Emlen and Miller, 1969). In species such as the Red-winged Blackbird (*Agelaius phoeniceus*), in which the breeding behavior of the sexes differs markedly, these factors probably pace the behavior of the female since she builds the nest, incubates, and cares for the nestlings. The male Redwing, however, is largely concerned with territorial defense during the breeding period and with rare exceptions is not directly involved in nest building, incubation, or feeding nestlings (Allen, 1914; Beer and Tibbits, 1950; and Orians, 1961). In the present report I present data which show that seasonal changes in the male's behavior occur and that these changes are correlated with seasonal changes in the difficulty he experiences in maintaining territory.

METHODS

The study was conducted on a small (16.5 acre) fresh-water marsh located near State College, Pennsylvania. The marsh was bounded on two sides by small creeks which served as the primary sources of ground water. The remaining side was bounded by dense bush oak and maple woods. The dominant vegetation was cattail (*Typha* sp.) in the wetter portions of the marsh and sedge (*Carex* sp.) in the dryer portions. The Redwing population on the marsh was isolated by hills and extensive cultivated areas.

I carried out the study through four complete breeding cycles (1966-1969). As many males as possible were captured using mist nets and Potter traps baited with corn. All captured birds were individually marked with leg bands of colored plastic tape. Territorial boundaries were determined by plotting the movements of each male on field maps followed by drawing an envelope around the outermost points.

Throughout one breeding season routine observations were made between the hours of 06:00 and 11:00 EST, on seven marked territorial males. I watched each bird for one or two periods of approximately one and a half hours in each of seven consecutive ten-day periods. The following data were recorded: the frequency of songs and calls; the frequency and durations of the periods when the male was on territory, off territory, on the ground on territory, perched on territory, and flying on territory; and the frequency and durations of all trespasses by conspecific males on the observed territory. Detailed data on the events and dates of the breeding seasons, presented in detail elsewhere (Peek, 1969), formed the basis for dividing the breeding season into functional periods (Fig. 4). Dates of the various events reported here agree well with those reported for the same

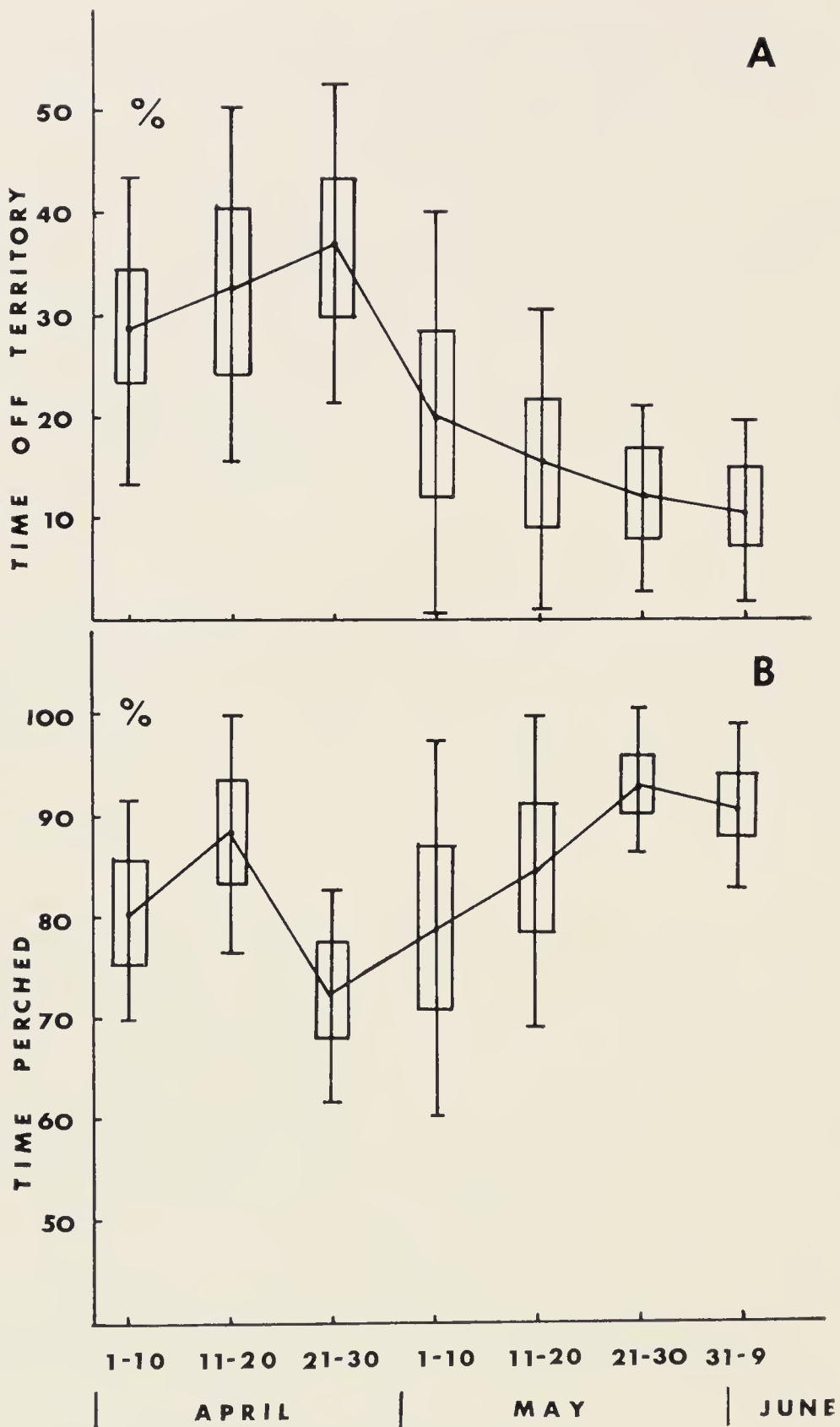


FIG. 1. A. Percentage of observation period the territorial male was off his territory. B. Percentage of time on territory that the territorial male was perched. Observation: between 06:00 and 11:00. Dots represent means; rectangles indicate mean \pm one standard error; brackets denote 95 per cent confidence intervals.

species in New York (Allen, 1914) and Wisconsin (Beer and Tibbits, 1950; and Nero, 1956a).

Three experimental manipulations of the population were made:

(1) Thirty-five territorial males were removed from their territories over the four breeding seasons at times distributed throughout each season. The date of removal was recorded and the identity of the new territory owner was determined.

(2) Twenty-three territorial males were surgically muted (by cutting the hypoglossal nerves controlling the syrinx) at times distributed throughout two breeding seasons. Immediately after the operation the muted birds were released upon their territories and their behavior as well as the behavior of conspecific males toward them and their territories was observed to determine the effect of their being unable to vocalize upon their ability to hold territory. The details of this and the following epaulet-coloration experiment are reported elsewhere (Peek, in press).

(3) The red epaulets of 17 territorial males were colored black (using Nyanzol B dye) or white (by feather clipping) at times distributed throughout two breeding seasons. The behavior of these birds as well as the behavior of conspecific males toward them and their territories was observed to determine the effect of reducing the effectiveness of their display upon their ability to hold territory.

The 95 per cent confidence limits were calculated from "t" values with the appropriate degrees of freedom.

RESULTS

Seasonal Activity of Normal Territorial Males.—A number of the activities of territorial males showed seasonal differences. Males tended to spend progressively more time off of the territory during April and spend progressively less time off territory during the remainder of the season (Fig. 1A). During the last 20 days of the season, males spent significantly ($P < 0.05$) less time off territory than during the last 10 days of April. During the course of 58 observation periods (mean duration 78.4 ± 3.3 minutes) the males were on territory an average of 73 per cent of the time (mean duration 57.4 ± 2.9 minutes). While on territory, males alternated between periods of perching and periods on the ground. While perched, the males spent most of their time singing and the rest preening or resting quietly. The mean percentage of the total time on territory that males spent perched decreased during the last of April and then gradually increased throughout the remainder of the season (Fig. 1B). Since little time was spent in flight, the difference between the percentage of time perched and 100 approximates the time the males were on the ground in the territory (primarily feeding).

Advertising song, which apparently functions in territory defense (Orians and Christman, 1968; and Peek, in press), was given throughout the breeding season. There was no significant change in the number of song bouts during the breeding season (mean 4.0 bouts per hour). The number of songs per bout (Fig. 2A) and the number of songs per unit time (Fig. 2B) both decreased significantly ($P < 0.05$) as the breeding season progressed. The song

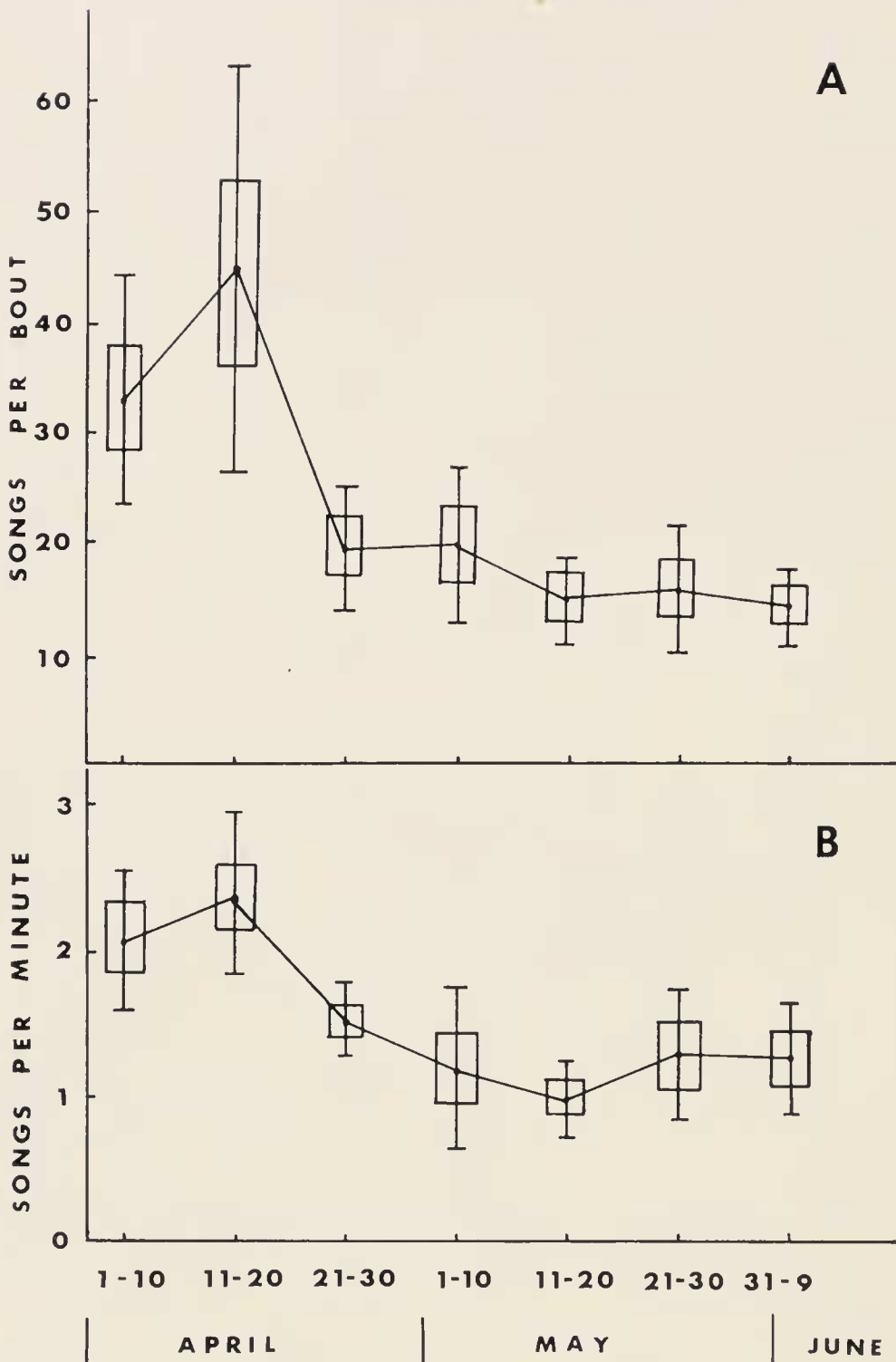


FIG. 2. A. Songs per bout of singing per territorial male. B. Songs per minute per territorial male. Observations between 06:00 and 11:00. Dots represent means; rectangles indicate mean \pm one standard error; brackets denote 95 per cent confidence intervals. A bout of song was defined as a group of consecutive songs, none of which was given more than 2.5 minutes apart.

rates reported here agree well with those reported for birds in the same marsh for the period 1 May–10 June 1960 (Vandenbergh and Davis, 1962). Allen (1914) reports for nearby Ithaca, New York, that Redwing song and display reach a peak about one week after the arrival of the resident females and that after mating occurs song gradually diminishes. The seasonal trend in song frequency reported by Beer and Tibbits (1950) for the Redwing in Wisconsin is very similar to that reported here (Fig. 2). The song frequencies, however, were all much higher than those reported here (their peak song rate in April was approximately nine per minute and by late May was still three per minute).

The greatest variation in the number of songs per bout occurred early in the breeding season when males gave as many as 179 or as few as four songs per bout in the course of one observation period. The variation in number of songs per bout as well as the total number of songs decreased throughout the remainder of the season. During the last 10-day period the greatest range of songs per bout during one observation period was from 35 to four. Song was most often given by perched males but was occasionally given on the wing. Seasonal changes in the frequency of the Song-spread display parallel the seasonal changes reported for song frequency (Fig. 2) since song is frequently accompanied by the Song-spread display.

Seasonal Change in Trespassing by Conspecific Males upon Occupied Territory.—The mean rate of trespassing by conspecific males upon occupied territories reached a peak of more than two per hour during the second 10 days of April (Fig. 3). From this peak the mean number of trespasses decreased significantly ($P < 0.05$) by the first 10 days of May. Trespassing remained at approximately the same low level throughout the remainder of the breeding season. A large proportion of the trespasses recorded during the last two 10-day periods was due to intrusions by immature males (62 per cent and 75 per cent, respectively). Territorial males generally paid little attention to these immature males. To my knowledge the only comparable data available on rates of trespassing are those of Patterson (1965) who reported rates of 30 trespasses per hour for the colonial nesting Black-headed Gull (*Larus ridibundus*). The situation reported here is quite different from that in a gull colony possibly because of differences in the nesting densities of the two species.

Seasonal Change in Occupation of Vacated Territories.—During the pre-mating portion of the season (from territory establishment until the last of April) vacated areas were quickly occupied by previously unestablished males (Table 1). During the remainder of the breeding season (the post-mating portion) neighboring males expanded their territories to include any vacated areas. Territories vacated late in the breeding season sometimes remained vacant. Other research on the same species suggests a similar pattern, though

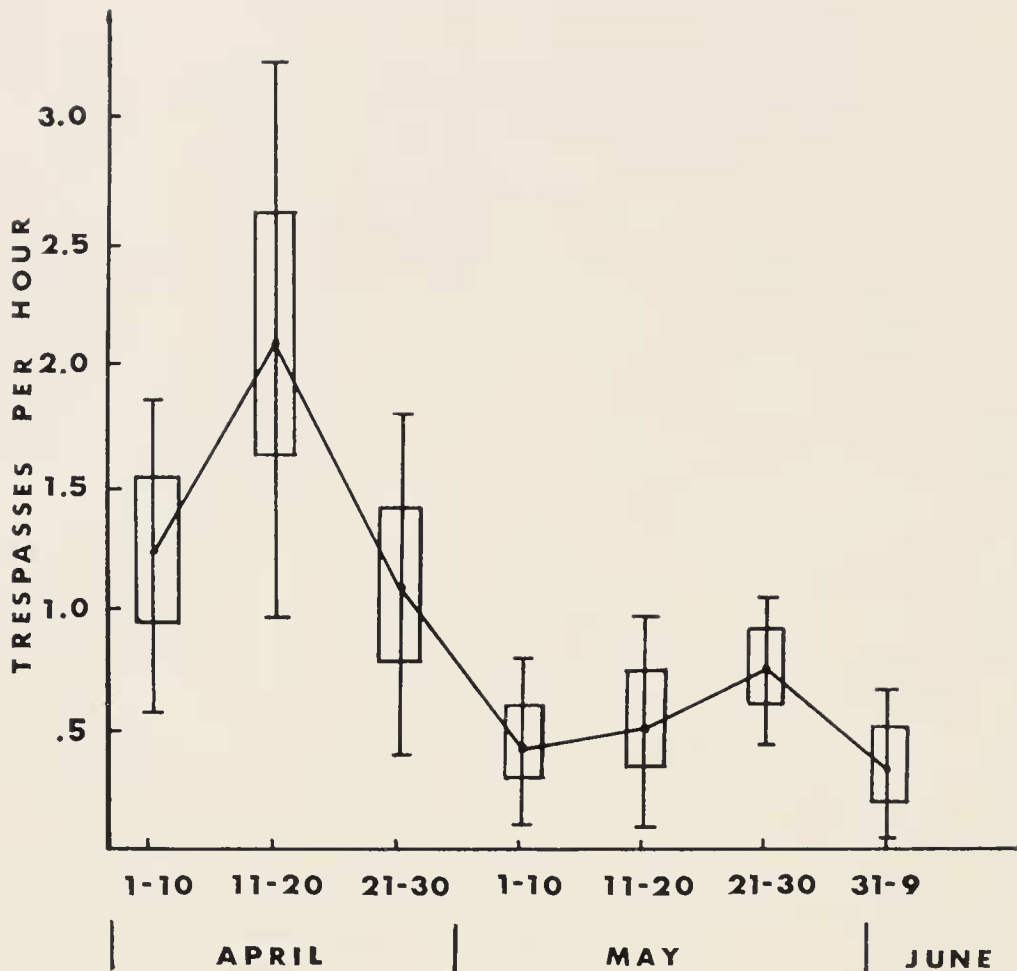


FIG. 3. Trespasses per hour by conspecific males upon occupied territories. Observations between 06:00 and 11:00. Dots represent means; rectangles indicate mean \pm one standard error; brackets denote 95 per cent confidence intervals.

most removals reported fall within the pre-mating period as defined here. In a study of this species in Wisconsin, Nero (1956*b*) reported 12 instances in which previously occupied territory was taken over wholly or partially by another male. In their study of a Redwing population in Wisconsin, Beer and Tibbits (1950, p. 66) found that, "If in the pre-nesting season a male is removed from his territory it is immediately taken over by either the adjoining males or a new male. Later in the season this is usually not the case." In removal experiments on the Redwing in California, (Orians 1961, Table 10) the number of replacements after successive removals declined throughout the breeding season. First year males which do not normally hold territories did so after removals late in the season.

In the present study vacated territories were rapidly occupied during the pre-mating portion of the breeding season. Frequent trespassing generally occurred shortly after a resident male was removed from his territory. For example, on 18 April between 08:00 and 09:00, 51 trespasses were recorded

TABLE 1

NUMBERS OF TERRITORIES VACATED (N) AND THEN OCCUPIED BY UNESTABLISHED MALES (UM) OR NEIGHBORING MALES (NM) DURING DIFFERENT PERIODS OF THE BREEDING SEASON

	Period of Breeding Season								
	Pre-mating 26 March—21 April occupied by			Mating—Post-mating 27 April—22 May occupied by			Terminal 5 June—12 June occupied by		
	N	UM	NM	N	UM	NM	N	UM	NM
1966	1	1	0	1	0	1	0	—	—
1967	4	4	0	8	0	8	2	0	0
1968	6	6	0	3	0	3	1	0	0
1969	8	7	1 ^a	1	0	1	0	—	—
Totals	19	18	1	13	0	13	3 ^b	0	0

^a Vacated territory occupied by neighbor on 18 April.

^b No males occupied these vacated territories.

on the territory of a male removed an hour earlier. The duration of individual trespasses was less than two minutes at this time. By the end of the three hours one previously unestablished male had succeeded in establishing himself on the territory and was successfully chasing off the now relatively few trespassers. During the post-mating period vacated territories were occupied more slowly. For example, on 14 May between 08:15 and 10:45 no trespassers were observed on the territory of a male removed approximately an hour earlier. At 10:45 one neighboring male entered the territory and remained for ten minutes. During the remainder of that day and most of the following day, he gradually increased the frequency and durations of his visits to the vacated territory and eventually occupied it.

Seasonal Change in the Ability of Muted and Epaulet-colored Males to Maintain Territory.—Males muted prior to 28 April consistently left their territories (Fig. 4). Three of the four birds muted during the transition period between 28 April and 1 May left their territories. Nine of the 10 birds muted after 2 May retained their territories. Though the territories of birds muted prior to 28 April were carefully watched (in some cases continuously for three days), no birds were seen to return to their territories. The failure of these birds to retain territories was probably a result of the rapid occupation of temporarily vacated territories by other males during this portion of the breeding season. The rate of trespassing upon the territories of three muted males (mean 1.9 trespasses per hour) during the transition period was significantly greater ($P < 0.05$) than that on the territories of normal males (mean 0.9 trespasses per hour).

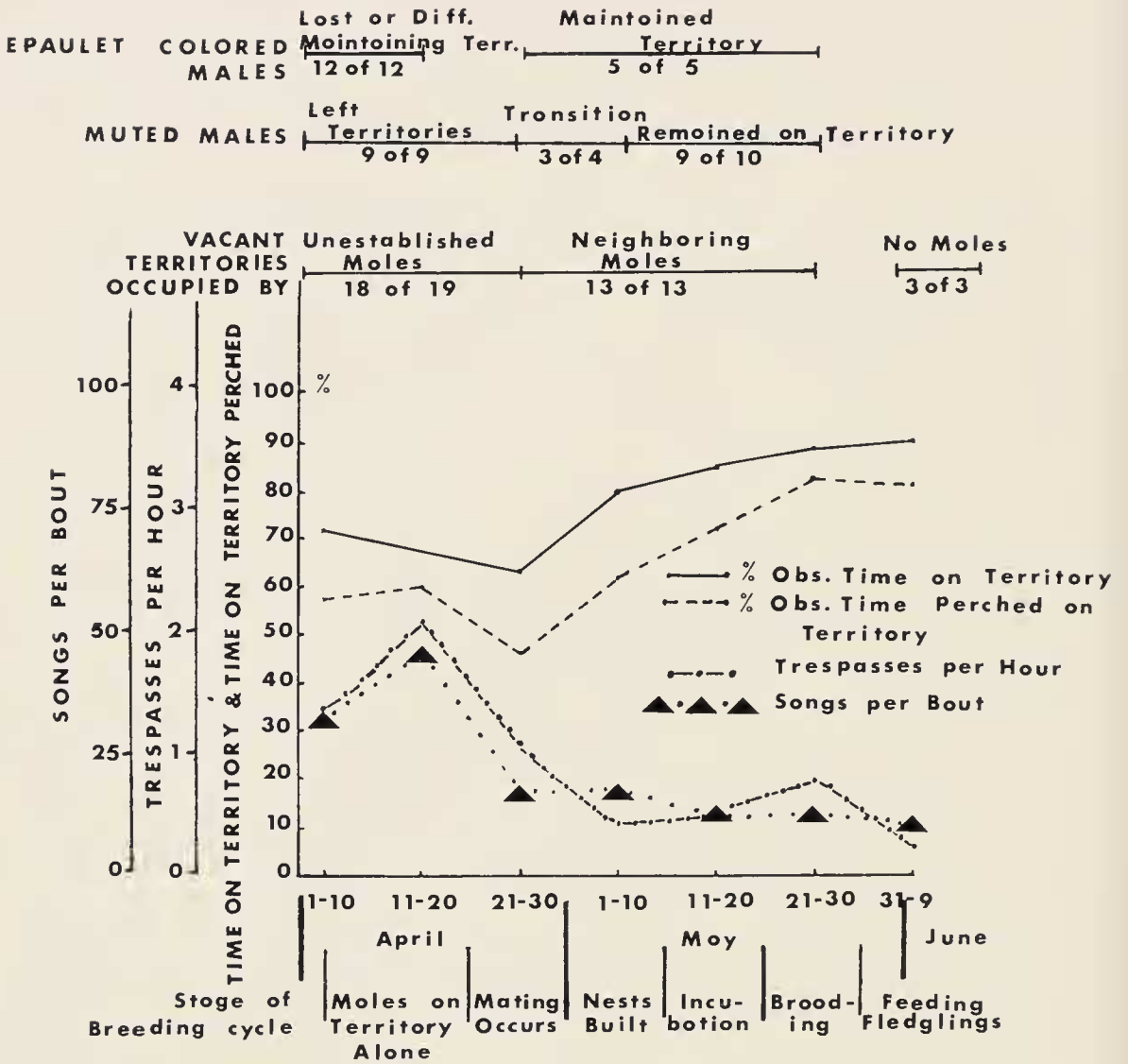


FIG. 4. Summary diagram of changes in the major aspects of the breeding behavior of the Red-winged Blackbird throughout a breeding season.

Males whose epaulets were altered before they had acquired mates (pre-mating period) lost all or part of their territories (Fig. 4). Trespass occurred at a significantly ($P < 0.05$) greater rate (mean 5.8 trespasses per hour) on the territories of experimental males than on the territories of normals (mean 0.9 trespasses per hour). Males whose epaulets were colored during the mating and post-mating period maintained all of their former territories, and one even enlarged its territory when an adjacent one was vacated.

Thus, muted and epaulet-colored males were either unable to maintain territory or had great difficulty in doing so during the period when territories are presumably being parceled out (the pre-mating period) but maintained their territories after this time (the post-mating period).

DISCUSSION

The principal findings of this study are summarized in Figure 4. Apparently a major shift occurred in many aspects of the breeding biology of the Red-winged Blackbird around the time of pair formation. This shift provided a basis for dividing the breeding season into two periods: (1) pre-mating and (2) post-mating.

The pre-mating period was a time when many aspects of intraspecific territoriality were at peak levels and spacing of the population was undoubtedly achieved. Throughout most of this period the territorial males spent approximately 75 per cent of their time on territory and were perched and generally singing an average of 80 per cent of this time. Song was given at peak rates during this period. Since intruding males were usually responded to with the Song-spread display, the peak in the trespassing rate at this time was paralleled by a corresponding peak in Song-spread display frequency. Competition for vacated territories was keen during the pre-mating period since all vacated space was rapidly occupied by unestablished males from some "free floating" surplus population. Later only neighboring males occupied vacated territories suggesting that unestablished birds had either left the marsh or for some reason no longer occupied available territory. Unestablished males accounted for much of the trespassing recorded during the pre-mating period, and their disappearance undoubtedly accounted for much of the decline observed in the trespassing rate. The competition for space was also reflected in the results of the muting and epaulet-coloration experiments which demonstrated that experimental males had more difficulty maintaining their territories during this period than did their normal neighbors.

During the post-mating period territorial behavior declined. Song, for example, was given at significantly lower rates. This decline in singing was paralleled by a decline in trespassing rates and the disappearance of the population of unestablished males. At this stage only neighboring males occupied vacated territory. Muted and epaulet-colored males were able to maintain their territories during this period indicating that vocalization and display of epaulets were no longer as vital to territory maintenance. Some of the data suggest that behavior associated with nest defense became more prominent during the post-mating period. Males spent progressively more time on territory and spent it perched in prominent places about the territory. Males were very sensitive to any disturbance; for example, a human being entering a territory evoked alarm calls at rates that sometimes exceeded 1000 per hour for periods of time in excess of an hour.

These results suggest that the role of the male Redwing changes as the breeding season progresses. Early in the season the emphasis is on intra-

specific territory defense to achieve spacing of the breeding population; later the emphasis shifts to interspecific defense and protection of the female, nest, and young. On the basis of studies of this species in Wisconsin, Beer and Tibbits (1950, p. 66) come to a similar conclusion, placing the occurrence of the shift around the start of egg laying. There is good evidence for a seasonal decline in behavior commonly associated with territoriality for the Black-capped Chickadee (*Parus atricapillus*) (Stefanski, 1967) (Dixon and Stefanski, 1970). In this species song functions solely in territorial contexts and not in the attraction of mates; therefore, the decline in singing during nest-building cannot be interpreted as indicating that mate attraction has ceased. I am not sure to what extent song in the Redwing functions in attracting mates and thus would be expected to decline at the time of mating. There are, however, a number of reasons (more fully presented elsewhere, Peek, in press) for believing song is importantly involved in territorial defense: (1) Muted males experience difficulty in maintaining territory and song appears to be the only vocalization which could play a major role in this respect; (2) song is given primarily only during the period that territory is maintained; and (3) song is given more frequently when trespassing rates are highest and decreases with decreasing trespassing rates.

During the post-mating portion of the breeding season the males apparently play a significant role in defending the territory against intrusion by other species. The presence of a human being on a territory containing an active nest evokes a strong response from the male (repeated diving upon the intruder and alarm calling at high rates with little decrement of the response over time). Allen (1914) noted that the male always shows great concern when the nest is approached. During the first portion of the season before the females have arrived, the territorial males seem much less concerned with human beings on territory; unfortunately no quantitative data is available to compare male responsiveness to a standard stimulus (e.g. a human being on territory) throughout the breeding season.

Preliminary data on the flushing response of nesting females of muted and normal males suggests that the alarm calls of the male function to alert the female of approaching danger. It was possible to approach the nest of a female on a muted male's territory much closer without flushing her than the nest of a female on a normal male's territory.

Many of the male Redwing's vocalizations are alarm calls, all of which are given frequently during the post-mating period. Of the nine vocalizations recorded during the course of the present study, six were clearly given in response to other species (especially the observer) intruding on the territory (these six vocalizations accounted for 63 per cent of the total of 16,015 vocalizations I recorded). Orians and Christman (1968) list 18 vocalizations given

by the male Redwing; nine of these, accounting for 59 per cent of the total of 7,200 vocalizations they recorded, were described as being given in response to intrusion by other species. Their data show that the female Redwing gives only four of the nine alarm calls listed for the male, further suggesting a specialized role for the male in guarding against interspecific intrusion upon the territory. Finally, I found that at this time the male spends more time on territory perched in prominent places presumably surveying his territory during the post-mating period and spends less time singing (Fig. 4). Clearly more quantitative data are needed to define the male's role in interspecific territory defense at all stages of the breeding season.

The presence of a population of unestablished males appears to be an important factor affecting the breeding behavior of the male Redwing. The existence of surplus populations of unestablished males during the breeding season is well-known for many birds (Hensley and Cope, 1951 and Stewart and Aldrich, 1951). Stewart and Aldrich noted that in those species just beginning their breeding cycle during the period of shooting, there were large differences in the numbers of males collected as compared to the number of females collected (as high as 15 males to one female). Approximately equal numbers of both sexes were collected from those species that were well into their breeding cycles during the shooting period. Thus, surplus males were available to occupy territory only during part of the breeding season. Holmes (1966) found that in the Dunlin (*Erolia alpina*) the territories of birds removed during the period of arrival on the breeding grounds were rapidly filled by new birds, but that later in the season they remained vacant even though territorial activity continued through this period.

One explanation for the failure of unestablished male Redwings to occupy vacated territories after the mating period to the extent they did prior to mating may be that most of them leave the breeding grounds around the time mating occurs. Beer and Tibbits (1950: 16) favor this explanation; they found that with the arrival of females (middle of April) excess males unable to obtain territories crowded into the marsh only to disappear later (the end of April). In an island population of Song Sparrows (*Melospiza melodia*) Tompa (1962) found an excess of 55 birds during the period of mating and final spacing. These excess birds definitely left the island when nesting began.

An alternative explanation is that excess birds remain in the area but are no longer disposed to trespass and occupy territory. In the present study three muted males who lost their territories later returned to them. None of these three marked birds was seen in the intervening period (over a month and a half in one case). This demonstrates that excess birds may well be in an area and not be detected by an observer constantly in that area. The fact that all of these birds reappeared on the same day that their former territories were

vacated suggests that they had been around the mash and were aware of the situation on it. Studies using improved biotelemetry techniques might eventually supply answers to present questions on surplus populations.

SUMMARY

Seasonal changes were found in a number of aspects of the breeding biology related to territory of the Red-winged Blackbird. There was a significant decrease in the frequency of male song, male Song-spread displays and in trespassing upon occupied territories at the time mating occurred. This shift in behavior was paralleled by a decrease in the difficulty with which behaviorally impaired males (muted or epaulet-colored) maintained their territories as the season advanced. Experiments of systematically removing birds from their territories suggest that the surplus population of males which was present on the marsh prior to the occurrence of mating disappeared after mating. It was concluded that prior to mating many aspects of territoriality were at peak levels, that spacing of the population was probably achieved at this time, and that the population or surplus males was a crucial factor at this time. After mating, many aspects of territorial behavior decreased in frequency and the surplus male population disappeared. During the post-mating portion of the breeding cycle males appeared to be primarily involved in defense of the female, eggs, and young from predation.

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